MORSE (ED. S.)

EMBRYOLOGY OF TEREBRATULINA.

BY EDWARD S. MORSE, PH.D.,

PROFESSOR OF COMPARATIVE ANATOMY ~~AND~~ ZOOLOGY IN BOWDOIN COLLEGE.

From the Memoirs of the Boston Society of Natural History, Vol. II.

EMBRYOLOGY OF TEREBRATULINA.

BY EDWARD S. MORSE, Ph.D.,

PROFESSOR OF COMPARATIVE ANATOMY AND ZOOLOGY IN BOWDOIN COLLEGE.

VIII. Embryology of Terebratulina. By Edward S. Morse.

WITH the great impulse given to the study of Zoölogy through the labors of Charles Darwin, renewed effort has been made to work up the embryology of those forms which have rendered so little satisfaction from the study of their mature characters, and thus through the labors of European naturalists new light has been thrown upon the developmental history of Sagitta, Amphioxus, the Tunicates, and many other aberrant groups. And now while the embryology of nearly every prominent group has been more or less studied, and important relations revealed that would have otherwise been obscured, little or nothing has been done to throw any light on the embryology of the Brachiopods, a class represented by thousands of species in past times, and one of which we have the earliest records in the rocks.

This dark portion in the history of the Brachiopods seems all the more strange when we recall the many beautiful monographs of various genera of Brachiopods published since Cuvier's famous memoir, in the year 1802, on Lingula, and when it is remembered that a hundred and more species still exist in the seas at present. What little has been accomplished in this field, however, has shed great light on the natural affinities of the class, and it may be well briefly to recall what has already been done in order to make this portion of their history more complete.

To Oscar Schmidt is due the credit of giving the first figure of a larval Brachiopod. In the "Zeitschrift für ges. Naturwissenschaften," 1854, p. 325, he gives a description of the embryo of some species of Terebratula collected in the North Sea. Accompanying this description a simple figure was given. In this the embryo shows a deep constriction in the centre, the free or cephalic portion being wider than the posterior half, which is abruptly truncate at the end, and he infers, and rightly too, that at this end the embryo becomes attached. I add a brief translation of his description.

> The embryos of the Norwegian Terebratula observed by me differ remarkably from the embryo Lingula as described by Owen. They resemble a *Euastrum* composed of unequal halves; the round end seems to be the anterior. The somewhat narrower hinder portion extends into two projections. In none of the ovaries examined by me — for in these were the embryos found — had the development gone farther. In the perfect ignorance in which we now are with regard to the development of Terebratula, every small contribution towards clearing up this question is acceptable.[1]

[1] The allusion to the embryo Lingula of Owen has reference to Prof. Owen's memoir on the Anatomy of Terebratulina, forming the introduction to Davidson's British Fossil Brachiopoda, published by the Palæontolographical Society, London. On Plate I. of the Introduction, Owen figures five eggs of *Lingula anatina*, which he supposes are impregnated ova. In one egg he suggests the rudiments of a peduncle. The egg, as it escapes from the ovary by dehiscence, often presents the appearance figured by him, from the thin membrane still adhering to the egg after its rupture, and consequent separation, from the cluster.

To Lacaze-Duthiers, however, is due the credit of first presenting several stages in the embryology of a Brachiopod. In a memoir [1] upon the curious form Thecidium, from the Mediterranean, he figures the egg, as well as several subsequent stages in the early history of the embryo. These were found in a pouch attached to the cirri and contained within the pallial cavity. The embryo is first divided into two transverse segments, then into three, and finally into four segments. In one embryo he found two red ocular points upon the cephalic ring, in another four red eye spots occurred.

In one figure he represents the rings contracted upon each other, as will be seen to be the case with the embryo of Terebratulina. As before, I shall give the reader a condensed translation of the paper.

The youngest egg studied had already a somewhat pyriform and elongated shape. The most striking fact was the size of the cells composing it, and which themselves enclosed a great quantity of granules of relatively very large size. The cells no doubt were the result of segmentation, and the granules must have appeared during the first movements of embryonic activity, for the vitellus had only very minute granules.

In the next stage frequently seen after the preceding, and which I have observed in the same lot of young, the embryo divided into two lobes, the larger being always attached to the *suspensory filament.* In the embryo so divided by a circular furrow, perpendicular to the longer axis, the mass has a yellow tint, and is no longer composed of large cells, but is filled with yellow granulations much finer, and enclosed in smaller cells. In the smaller lobe a clearer space is seen, where the cells are filled with nearly colorless granules. On each side of the larger lobe also, and very near the transverse furrow, are two transparent spaces smaller than the preceding, but similar in other respects.

The larger lobe, attached, as stated, to the *suspensory filament,* is the anterior; the faces cannot yet be distinguished; but later it is possible to recognize the superior or inferior aspect.

The development, therefore, commences by the appearance of the two lobes, one the anterior, with two white spots, and the other with a single clear spot; later other spots with less coloring matter appear. Thus there appears near the point of attachment, on each side of the peduncle, a clear white spot, then the two lateral, spots above referred to, grow longer and obliquely extend towards the centre of the lobe.

Between these two last spots, on the line of separation between the lobes, the colored granules accumulate and form these lobules, the median later extending toward the posterior lobe.

The posterior lobe itself does not increase in proportion to the rest of the embryonic mass, but the transparent spot begins to show what it will later become. It extends towards the place where the lobules commence, then it becomes depressed in the middle, and will form, in fact, a real depression. There is still a gap between this and the succeeding stage to be described. The two white lateral bands, near the separation of the lobes, are traces of the formation of a new lobe, for the anterior lobe divides into two by a transverse furrow, and these two anterior lobes always remain relatively very large, the posterior changing but little.

At the time when this division takes place, toward the point of attachment where two other little clear spots have been seen, a lobule rises, which forms the counterpart of the little primitive posterior lobe. Thus the embryo is composed of four portions, two large in the middle and two smaller at the ends.

If the embryo is examined on all sides, it is soon seen that the two poles of the ovoid embryo are bent towards each other on one side, as if the two anterior lobes were curved over towards the two posterior. The concave face may be considered as the inferior, and the convex, the dorsal aspect.

The insertion of the suspensory peduncle is on the dorsal side of the anterior extremity, on the back of the little anterior lobule, not far from the edge of the second lobe. This peduncle is cellular, and composed of very distinct elements, and easy to recognize. The embryo is, therefore, suspended by the back of the head.

The inferior side of the anterior lobule is flat and somewhat quadrilateral in the most developed embryo seen; near the middle is a sort of oval longitudinal slit, which appears to be the mouth, although I have never seen particles of coloring matter, which I have put into the surrounding liquid, penetrate this opening, but indeed the embryos are still too young to feed.

[1] Annales des Sci. Nat., 4^e^ Serie, Vol. xv., p. 317.

On the inferior side also of the lobule, somewhat deeply seated in the tissues, appear some red dots symmetrically placed on each side. These spots I believe to be eye spots; they are sometimes four in number, and sometimes only two. The presence of these spots and of the slit, lead me to consider this extremity as anterior.

The second, or large, anterior lobe is swollen behind, and nearly flat beneath. Its posterior edges run obliquely backward to form a very obtuse angle, hardly closed on the ventral side of the large posterior lobe, extending towards the angle made by the posterior lobule, which seems to be hollowed out with a wide depression.

The embryos, when the peduncle is broken, swim and whirl round by means of the cilia clothing the lobes. The anterior extremity moves forward always. The embryos are very contractile, so that, often on meeting an obstacle the longitudinal diameter becomes shorter than the transverse, the two extremities contracting towards each other. The cilia then stop and seem to disappear.

It has not been possible to carry the observations farther.

To sum up, then, on the inferior aspect one of the most advanced embryos shows four eye dots, as well as a distribution of the yellow material in the midst of the large anterior lobe, which reminds one much of the origin of the liver in the Acephala or Gasteropoda, and it is probable that the alimentary tract is hollowed out in the middle of these yellow granules, so that the secretory lobules of the liver of the adult Thecidium are foreshadowed in these series of little packets.

In the early summer of 1872 I was fortunate in tracing the embryology of Terebratulina so far as to carry the embryo to a form with three well marked and deeply constricted segments, and saw enough at that time to convince me that the embryo became attached by its caudal segment. These meagre results were published in Silliman's Journal.[1]

Some interesting features, however, had been brought to light in studying the early stages of certain Brachiopoda, the most important of which were presented by Fritz Müller in a note published in Reichert und Du Bois-Reymond's Archiv, 1860, p. 72, and a subsequent note in Wiegmann's Archiv, 1861, p. 53. These notes referred to the early stages of a form supposed to be Discina, collected at Santa Catharina, Brazil. I subjoin the notices which were published in the Annals and Magazine of Natural History, 3d series, Vol. VI., p. 310.

"Dr. F. Müller has sent from Brazil the description of a larva belonging undoubtedly to a Brachiopod, which is the more interesting, as the Brachiopoda are the only Mollusca regarding the development of which we have no information.

"The larva in question is a small, perfectly orbicular, bivalve Mollusk. The two valves are similar, but unequal in size, the dorsal valve being the largest. At the place of the hinge a small oval plate is placed transversely between the two valves of the shell. The mantle is gaping all round. Five pairs of very stiff setæ, of which one is much stronger than the others, and curved backwards, project at the periphery. They originate in the mantle of the ventral half; at least this is the case with four of them. A series of finer setæ spring from the circumference of the mantle of the dorsal valve, and curve down upon the outside of the ventral valve. The animal, as well as the shell, would be divided into two symmetrical halves by a plane drawn vertically through the middle of the hinge. The body, which is furnished with an alimentary canal, two auditory capsules, and two eyes, fills the posterior half of the space between the valves. The anterior half is occupied by four pair of cylindrical arms, between which a rounded knob is situated. Behind the knob the mouth is perceptible.

"These four pair of arms are supported upon a common peduncle, at the extremity of which, therefore, the mouth is placed. The arms are covered with a very well developed ciliary coat, by the agency of which the little animal swims. The reproductive and circulatory organs are wanting.

"During natation the mouth is always directed forwards, which is in favor of the generally received opinion

[1] Am. Jour. Science and Arts, IV., 1872, 262.

as to the anterior and posterior regions in the Brachiopoda. It is, in fact, now evident that the Brachiopods are *depressed* animals, having an anterior or ventral, and a posterior or dorsal valve. MM. Agassiz and Vogt are therefore wrong in regarding them as *compressed* animals like the Lamellibranchiate Mollusks; that is to say, as animals having a right and left valve.

"The larva, moreover, can not only swim, but also creep. This latter mode of progression is effected by a sort of rotation of the ventral valve alternating to the right and left. In this movement the animal pushes by supporting itself principally upon the strongest of the bristles above mentioned."

In Wiegmann's Archiv, Dr. Müller communicates additional observations on the larval Discina, a notice of which follows from the Annals and Magazine of Natural History, 3d Series, Vol. VIII., p. 505.

"In the Annals for October, 1860, p. 310, we gave a short abstract of a description of the larva of a Brachiopod observed by Dr. F. Müller at Santa Catharina, on the coast of Brazil; he now adds some further details from repeated observations in the summers of 1859 and 1860. The larva appears to occur late in the summer, from February to April.

"When the little animals are placed in good-sized vessels with pure sea-water, they soon ascend slowly; the slightly gaping shells stand perpendicularly, the hinge-margin downward; close to the anterior margin the eight arms spread out horizontally like rays, with their tips slightly bent downwards; and the roundish knob situated between the uppermost pair projects beyond the plane of the arms. In this posture they move slowly about near the surface. When strongly shaken, or sometimes without any perceptible reason, they retract the arms and close the shells, which then slowly turn over and sink to the bottom with the free margin downwards. If the arms be again protruded, the hinge-margin also again turns downwards.

"The duration of this state never exceeded five to six days, and in general the larvæ adhered to the bottom or sides of the vessel in a still shorter time. When they adhered to the sides, the mouth was always directed downwards; the ventral shell was strongly drawn forward until its anterior margin reached or passed that of the dorsal shell; the transversely oval plate, previously concealed within the shells (the peduncle), was protruded, apparently twisting around the notched hinder margin of the ventral shell, so that its anterior margin became posterior. For a day or more the animal remains contracted and quiet; then, the shells being slightly opened, the arms are half extended, and strike inwards, one or more at a time, just as in the marine Bryozoa. In a few days new bristles appear at the anterior margin, in the space left between the more delicate setæ of the dorsal shell. In a week the author counted twenty of these, mostly belonging to the dorsal shell. The longest were 0.8 mill. in length, straight, colorless, 0.006 mill. in thickness at the base, terminating in a fine point, unjointed and distantly feathered with fine lateral setæ 0.02 mill. in length. The principal change in the soft parts consisted in the retrogression of the organs of sense. The eyes had become broken up into groups of about ten black points; the previously spherical auditory vescicles were shrunken into longish sacs, closely surrounding the otoliths. In somewhat older animals there was no trace of the organs of sense, although they had not lost their sensibility to light.

"One of the larvæ lived for a month after its adhesion; but from the lapse of a day before its death was noticed, the soft parts had become greatly decomposed. The older bristles of the free larvæ appeared to be still present, as also the plumose bristles of the anterior margin. Besides these, there were on each side, about in the middle between the median line and the origin of the great bristles of the fourth pair, straight, smooth bristles, 0.2 mill. in length, projecting obliquely backward, little thicker than the strong posterior setæ, but with a much stronger outline.

"It is remarkable that in two years the author has repeatedly captured free-swimming larvæ which had evidently advanced further in their development than the oldest of those which had already fixed themselves. They were all destitute of the transversely oval plate, and of every trace of organs of sense; the plumose setæ of the anterior margin were also wanting, as were, more or less entirely, the older bristles. Of the more delicate bent bristles, some were usually still present, and these appeared to be unabbreviated, so that the missing ones had probably been lost by shedding. The stronger bristles, on the contrary, are gradually absorbed at the base; at least this is the case with the fourth pair; these were repeatedly met with of about half their proper length; the stalk, with its fusiform dilatations, had disappeared, while the apex remained readily recognizable by its peculiar curvature and denticulation. In a still older animal about a fifth of the length was still present, so that it no longer extended beyond the margin of the shell. This animal (the oldest examined by the author) had lost all the older setæ, except the small residue. On the other hand, the two straight, smooth bristles, which in the oldest attached animals scarcely began to protrude from the shell,

had attained a length of double the diameter of the shell, and being inserted into thick muscular sheaths were strongly and rapidly moved by the animal, sometimes spread out horizontally, sometimes again crossed backwards.

"During this complete change of the setæ the soft parts had undergone no essential alterations. The roundish stomach, reaching from the front to the middle of the longitudinal diameter, still showed the two dark spots of the young larvæ, which remind one of the similar spots in the larvæ of some Bryozoa. From the back of the stomach sprang the intestine, which bends under the margin of the stomach to the right, and then forwards, terminating about the middle of its right side. The œsophagus goes from the front of the stomach straight forward half way to the front of the shell, and then bends downward, so that the mouth lies close to the stomach. The arms, especially the two middle pair, had become longer and slenderer, and the knob between the anterior pair had diminished in size. No vessels or pulsating heart were recognized. — Wiegmann's Archiv, p. 53, 1861."

In the year 1869 I communicated to the American Association for the Advancement of Science the results of a study of the early stages of *Terebratulina septentrionalis,* made at Eastport, Me., in the early part of that year. This was afterward published in the Memoirs of the Boston Society of Natural History, accompanied by two plates.

In this memoir I showed the incipient cirri, seven or eight in number, and the gradual development of the complicated arms, the unfolding of the hepatic cœca from two folds upon the walls of the digestive cavity, the character of the shell structure, etc. And these two papers comprised all that has yet been done as to the early stages of the class.

A wide gap, however, has existed between the free swimming Annelidan larva clothed with cilia and the attached form revealing its Brachiopodan character in the presence of a dorsal and ventral plate, and the presence of cirri. After repeated visits to Eastport, almost solely for this purpose, I have at last succeeded in closing this gap, and in this paper I hope to make plain the history of the development of the dorsal and ventral areas, the peduncular attachment, and the relations the different parts of the mature animal bear to the embryonic segments, as well as to present some new features in the early stages of the species.

For two seasons I have found Terebratulina spawning at Eastport during the last of May and the early part of June. It is probable that they spawn through the season, since I have found them depositing eggs in April. At my request Mr. Rathbun made several observations during the summer, to ascertain how long the species continues to ovulate, and he informs me that on the only dates he collected them, namely, June 26, July 12 and Aug. 29, they were freely discharging their eggs. It is best, however, to study them as early in the season as possible, as the water in which the eggs develope must be kept at a low temperature, and this essential condition can be most easily accomplished at Eastport in May, where the temperature at that time ranges from forty to sixty degrees Fahrenheit.

The manner in which I secured the eggs for study was simple enough. Several shallow glass dishes were prepared by painting the bottoms black. Having dredged a lot of specimens, I arranged them in a circle around the edges of the dish, with their anterior ends pointing toward the centre of the dish. By arranging the specimens in this manner the difference in the sexes becomes at once apparent.

The eggs are discharged from the anterior margin and drop just beyond the pallial membrane, hanging in clusters from the setæ, and covering the bottom of the dish in the immediate vicinity of the animal, presenting the appearance of a white powder, though with a simple lens the individual eggs are plainly seen. They are opaque and spermaceti white in

color. In the course of a few hours they become clothed with cilia, and while many of them slowly move away, some remain and perish, or, at least, show no sign of development. These are probably not fertilized.

The sexes are separate, and the spermatozoa are discharged by the males in the same way that the eggs are discharged by the female, but whether the eggs are fertilized after they have left the parent, or before, I was not able to determine, as different lots of eggs behaved differently after their escape. In some cases the eggs did not appear to be locomotive until two or three days after their discharge, while in other cases they became active on the day of their discharge.

Great care must be taken to change the water every day, since the water soon becomes vitiated, and Paramæcia rapidly develope and appear to feed upon the embryos. The temperature of the water must be kept as near as possible to that from which they were taken. In drawing and replacing the water a glass syphon was found the best, as in this way the embryos were not disturbed, though some skill was required during the active natatory condition of the embryos, to prevent them from leaving the dish also.

The development of the embryo presents a series of well defined stages, and I shall consider each stage in turn. In the first stage the embryo becomes widened at one end. The segments are barely indicated, the posterior end is the widest, the anterior portion is ornamented with a conspicuous tuft of long cilia, so peculiar to the embryos of many worms. The embryo is also clothed with vibratile cilia, and in this condition slowly moves along the bottom of the dish without rising from it, or remains quiet. In the second well marked stage the embryo is divided into two prominent segments, these expand and contract upon each other slightly, and the cephalic segment has the power of partially bending from side to side. In this stage the embryo is most active, swimming rapidly in every direction and turning abruptly about. The œsophagus also becomes dimly defined. In the third stage the peduncular segment is developed and projects from the posterior portion of what can now be called the thoracic segment. At this stage the embryo either remains immovable upon the bottom of the dish or slowly moves about. In two cases delicately barbed setæ to the number of thirty-five projected directly backward from the peduncular segment. In the fourth stage the embryo becomes attached by means of its peduncular segment. The embryo is still clothed with cilia, though the long pencil of cilia has disappeared. The head is closely drawn to the thoracic segment, which becomes wider in transverse diameter, so as nearly to hide the peduncle. In the fifth stage the thoracic ring commences to fold, or turn upward upon opposite surfaces of its circumference, so as to gradually enclose the head; one fold being made slightly in advance of the other represents the larger or ventral valve. In this stage appear clusters of barbed and deciduous setæ upon the anterior margin, and in a later portion of this stage the first hardened areas of the dorsal and ventral plates make their appearance, and the cirri appear as blunted papillæ about the mouth. In the sixth stage the shell becomes rounded, the peculiar scaled structure makes its appearance, and the formation of tubules perforating the shell, and permanent setæ takes place.

In another memoir I hope to present the characters of the genitalia of the Brachiopoda. I will state here, however, that the eggs not only fill the large pallial sinuses, but hang in clusters from the genital band; from these parts they escape by dehiscence, and float freely in the perivisceral cavity. The anterior perivisceral wall is sufficiently trans-

parent to allow one to watch the eggs as they are gradually drawn to the infundibuliform orifices of the oviducts, and to secure them as they escape by the external orifice of the oviduct. In parting the shells for this purpose great care must be taken not to open them too far, as the parietal wall will rupture, and from this opening the perivisceral fluid and eggs will escape. The eggs are not uniform either in shape or size, though a distinct granulated membrane, the ovishell, is formed while the egg is contained in the perivisceral cavity. Segmentation is next seen, first as a few indentations upon the periphery of the egg, until finally the whole egg presents a mass of cells, as shown in Fig. 11. The egg next assumes an oval shape, becomes ciliated, and in several eggs at this stage a dim opening extending to the centre midway between the opposite poles of the egg was seen — whether this was the micropyle or the scar from which the egg escaped from the ovisac I could not determine; gradually the egg becomes widened at one end, which is to be the base, or posterior pole of the embryo. A long pencil of cilia springs from the smaller anterior end, so characteristic of the Annelid embryo.

First Stage. From some of my drawings it would seem as if the peduncular ring consisted of the primary posterior pole of the egg, the thoracic ring widening and enclosing it. At all events the thoracic ring forms the widest portion of the embryo, directly in front of which a second fold makes its appearance. Whether this is an indication of another ring I could not make out; later, however, it merges into the base of what is to be the cephalic ring, and the deep constriction that is soon to follow occurs between this fold and the thoracic ring. An end view shows the thoracic ring slightly flattened while the cephalic ring preserves its circular outline. In this condition the embryo swims slowly about. This ends the first stage.

Second Stage. In this stage, and one that seemed of the longest duration, a matter of three or four days, the embryo is quite elongated, and is divided by a deep, transverse line into two unequal halves, the head segment being the smallest. At this stage it is the most active, no longer moving slowly along the bottom of the dish, or remaining motionless, but ceaselessly swimming in a rapid manner back and forth through the water, and abruptly turning about; the segments expanding and contracting upon each other, and the head bending from side to side, the thoracic segment often being transversely wrinkled by this bending. A peculiarity of the embryo at this stage consists in the various external outlines assumed by the embryo, presenting also different proportions, as shown in Figs. 18, 19, 20 and 21, drawn from the same embryo. The first definite trace of internal structure now occurs in the formation of the alimentary tract, appearing as a long, narrow tract running from the thoracic to the cephalic ring, closed posteriorly, but blending with the cell contents of the cephalic segment. A clear interspace is also seen at the anterior portion of the thoracic ring. What appeared to be an opening in the posterior end of the embryo was seen in some cases.

During all these stages, from the egg upward, great difficulty arises in making out any feature of internal structure, owing not only to the minute size of the objects, but to their opacity, and what little has been made out has in most cases been done by slightly compressing the embryo.

During this active swimming stage in some embryos is seen a structure that appears to be the incipient peduncular segment. In Plate VIII., Fig. 25, and Plate IX., Fig. 78, a rounded process is seen protruding from the thoracic segment, the walls of which extend as far as

the division between the two segments. The alimentary tract is seen here, its anterior portion blending with the cell contents of the cephalic ring, while posteriorly it hangs in the cavity supposed to be the incipient peduncular segment. Whether this is the proper interpretation I cannot say, and the difficulty arises from the fact that in some embryos farther advanced this structure does not appear. Thus in Fig. 83, Plate IX., an embryo is shown in which no sign of the peduncle appears, and yet it seems in advance of the one just described, in showing the widening of the thoracic ring, one side of which shows a bulging which represents the future ventral fold. An irregular cavity is thus left by the bulging of the external wall, and in this cavity at a later stage I have seen the circulation of minute granules. Within this cavity is another cavity bordered by thick walls which hang from the suture dividing the two segments. The alimentary tract is seen suspended between the two segments, and showing a faint connection with this cavity. The cephalic segment shows no change in its granular contents save the presence of the alimentary tract. The parts surrounding this tract are continually contracting in a spasmodic way, though no trace of a muscular band could be detected. The interpretation of these cavities has perplexed me exceedingly. The most reasonable supposition is that the outside cavity in the thoracic ring marked *pl.* represents the cavity from which the pallial sinuses are to arise; in this cavity I observed the circulation of minute granules, as before stated. The cavity within surrounded by thick walls is the peduncular cavity, and a faint interspace running from the upper part of this cavity to the base of the digestive tract appears to be the opening up of the peduncular cavity into the cephalic segment, a cavity in which the stomach is afterwards to be suspended, and this may be called the perivisceral cavity. In Lingula and Discina the peduncular and perivisceral cavities are in open communication. In Discina the large azygos opening is very apparent. Future study will undoubtedly modify the interpretation of these cavities, and possibly show it to be altogether wrong.

In the hundreds of embryos examined, a few only were of sufficient transparency to reveal any structure within, and from this stage onward, the difficulty in this respect increases, as the embryo becomes more opaque, and with the after formation of the dorsal and ventral plates, combined with their minute size, render the study of their internal structure almost hopeless. Plate IX., Fig. 86, represents the peduncular portion just ready to protrude.

Third Stage. In this stage the peduncular segment has made its appearance as a rounded knob, varying in size in different embryos. Soon after the appearance of the peduncle, granules are seen gathering about its end, apparently adhering to the mucus secreted by it. Soon afterward adhesion takes place, the embryo remaining fixed when the water is disturbed, though even before the embryo becomes attached, the bulging of the thoracic ring becomes more conspicuous, leaving a clear cavity within. The walls of this bulging portion present a number of highly refractive granules scattered evenly over its surface. This portion first loses its cilia (Plate IX., Fig. 87) just before attachment; the embryo becomes sluggish, or at least, in most cases, ceases to swim actively. In two cases a cluster of delicately barbed setæ, to the number of thirty-five, was seen to project directly backward from the posterior end (Plate IX., Fig. 79). That these were very transient is evident from the fact that they were only observed in two cases out of three hundred and fifty-two different embryos examined. The head continues to move freely, and shows a slight fold at its base. As the head contracts, the thoracic ring widens; this is shown in Plate I., Figs. 42, 43, where the same is sketched with the segments extended and

contracted. In many embryos the thoracic ring presents an indentation on one side, as if the ring were a band partially uniting at this place. The peduncle gradually widens at the end into a sucking disk, and at this time the embryo becomes permanently attached.

Fourth Stage. The embryo now settles down upon its base of attachment, the thoracic segment widening and flattening, and appearing pressed to its point of support, so as to conceal the peduncle. The head is closely pressed to the thoracic segment, the clear space within having disappeared, and the head only appearing ciliated. And now commences the most important portion of the developmental history, in which, for the first time, we become acquainted with the development of the dorsal and ventral plates.

Fifth Stage. The thoracic segment commences to fold upon both sides of the head, and these are the dorsal and ventral folds. Gradually the head is enclosed by the folds. In this portion of their history I was peculiarly fortunate in securing hundreds of examples just after they had become attached to adult Terebratulina. These I studied in their natural positions. In some cases the Terebratulina had been torn from Mytilus, to which they had been attached. The peduncular disk brought away a layer of the black epidermis of the Mytilus, and to this surface many embryos conveniently became attached, and against this black background the pure white embryo showed to the best advantage. At intervals the Terebratulina would twirl its peduncle, thus presenting the embryos in different positions, all of which I instantly sketched. I have a great many drawings at every stage of this interesting growth, some of which are given on Plate VIII., Figs. 47 to 77, inclusive.

One fold grows more rapidly than the other, and I infer that this is to be the larger or ventral plate. The head appears to be gradually engulfed, as it were, though for a long time protruding beyond the dorsal and ventral folds. The folds also present for a long time a thickened and rounded border. The inner edge of what I suppose to be the dorsal valve, shows a distinct notch in the median line in some (Plate VIII., Fig. 63). As the dorsal and ventral folds develop, the embryo becomes elevated upon the peduncular stalk, and the attachment becomes so firm that a forcible stream of water falling upon them does not detach them, indeed a point of a needle, or a stiff camel's hair pencil, was found necessary for the purpose, and in the removal, the parts were so soft as to break down in most cases. The mouth also makes its appearance at this time, the head for a long time occupying the area enclosed by the two folds. As soon as the embryo rises upon its peduncle it drops partially over to one side, the ventral or larger area being uppermost.

The hinge margin is broad and slightly rounded when looked at from above; a side view, however, presents a wide and flattened area, as is shown in some species of Spirifer, and the embryo for a long time assumes the position that the Spirifer must have assumed. The dorsal and ventral folds close up on the sides, and their edges become sharper; the future lateral openings of the shell gradually extend to the base. From above, the thorax is wider than long. Starting from a broad base it widens gradually to the anterior margin, which is nearly straight, to which it joins by a short curve. A heart-shaped corneous shell is formed even at this early stage, for in several cases I met with it where the softer portions had been removed by Paramæcia. (See Plate VIII., Fig. 68.)

Before the folds have closed over the head, four bundles of setæ appear; one bundle containing from seven to nine setæ springing from where the folds unite laterally. These stand out at nearly right angles to the longitudinal axis. The other bundles containing from two to four setæ, spring from a point midway between the first bundles and the

median line anterior. Thus the embryo possesses from twenty to twenty-five setæ springing from the anterior margin. The larger and lateral bundles of setæ are the first to make their appearance. They are nearly as long as the entire length of the embryo, and are *delicately barbed and deciduous*. Upon pressure of the embryo they readily separate from their base of attachment. The dorsal valve is flattened, while the ventral valve is rounded, as before remarked. The first evidence of hardened plates appears in the later stages of these forms, for upon crushing the embryo in the live cage a number of angular fractures appear. (Plate II., Figs. 89 and 91.)

Fig. 85, Plate II., presents a view of an advanced stage, in which the relative position and character of the deciduous setæ are shown.

Fig. 81, just above, represents the same embryo as it appeared when slightly crushed. The manner in which the contents burst out from the shell still held by the membrane, as in a sac, the fracture of the shell and the detached setæ, are all instructive. Besides the minute granules which make up the substance of the embryo, larger cells, to the number of twenty-five or more, are seen scattered through the mass. In a slightly advanced stage, Fig. 90, Plate II., the mouth shows on each side a rounded papilla, the first appearance of the cirri. The mouth is prominent, and flush with the anterior borders of the pallial membrane; this is also shown in Fig. 82.

Fig. 91 represents the appearance of Fig. 90 crushed. Here the incipient cirri show as two prominences, one upon each side of the mouth. The shell fracture is also more apparent. As the embryo advances in growth the outline changes, having at first a transversely semicircular outline with the posterior margin straight, as in Leptæna. It gradually elongates, and commences to widen its anterior margin, as in Fig. 93; it becomes well rounded as in Fig. 88, and at this time is seen a difference in the length of the dorsal and ventral plate, and for the first time appear concentric lines of growth. The deciduous setæ, at this stage, separate at the slightest handling of the embryo, and as in every case the figures on the plates are exact fac-similes of my original drawings, the setæ are not shown in Fig. 88, as they dropped off in removing the specimen to the live box. A stage of the same age, or slightly later, is shown in Fig. 94, and this stage immediately precedes the formation of the scaled structure of the shell. Its outline is quite unlike any adult Brachiopod known. It is longer than broad. The posterior margin is quite broad and rounded. The anterior margin is twice the breadth of the hinder margin, semicircular, and abruptly rounded where it meets the lateral margins, which are incurved. The larger bundles of setæ project at the point where the anterior curved margin joins the lateral margin. (See Fig. 94.) A distinct triangular area is seen within, which represents the head, below which the digestive tract is faintly indicated.

Sixth Stage. The embryo has now discarded its deciduous setæ, and for the first time the permanent setæ make their appearance, as well as the peculiar scaled structure of the calcareous shell, and with these new features that of the peculiar tubules perforating the shell must be added.

Fig. 96 represents a somewhat more advanced stage than Fig. 94. The form is now bluntly oval, its posterior margin prominent and bluntly rounded. In general contour it recalls Siphonotreta, placed in the family Discinidæ by Davidson, a genus not occurring above the Silurian. Seven prominent setæ longer than the shell now spring and diverge from the anterior margin. These are not barbed. The shell now plainly shows its scaled

structure, and within is seen four cirri, below which the digestive cavity occurs. The tubules first formed are three in number, of large size, and are arranged in a triangular figure, the two forming the base of the triangle occurring midway between the front and hinder portions of the head, the other tubule being near the anterior margin.

The tubules, or pores first formed, present some new and interesting features. In every case examined, the first that make their appearance are three in number, and are invariably arranged so as to form a triangle as shown in Figures 95, 96 and 105. They are also much larger than those subsequently formed. They are oval in shape, and within their borders a circular, granulated plug of a reddish yellow color is seen, between which and the outer border of the tubule a clear space is visible. From twelve to fourteen hairs of various lengths, some of them three times as long as the diameter of the pore, spring from the margin of the granulated disk, and radiate in every direction. That these are veritable hairs and not minute tubules in the shell, or any internal markings, I proved in a very simple manner. First I made an exceedingly careful drawing of the tubule, showing exactly the position of each hair, and then brushing the pores slightly with a delicate camel's hair pencil I again made a careful drawing of the same pores, using the same objective, $\frac{1}{5}$ Wales. The hairs were found in every case to have changed positions, being bent in different directions. Fig. 100, *a*, represents a drawing of the tubule before brushing, though in this the hairs were bent in handling the specimen, and Fig. 100, *b*, represents the same pore after brushing. Next summer I hope to study this peculiar structure of the tubule with higher powers. The tubules subsequently formed are much smaller in size, showing, however, the same hairs in less number radiating from them.

Whether there is any relation between these veritable hairs and the radiating lines surrounding the tubules, as described by Queckett and Carpenter, and regarded by them at one time as representing cilia, I cannot say. In this connection, however, it is interesting to recall other views on the subject.[1] It is more probable that the tubules are simply organs of general sensibility. In the test of Crustacea similar tubules occur, which penetrate to the vascular layer beneath, and are regarded as endowing the test with a general sensibility.[2] The subsequent tubules appear to make their appearance in a certain symmetrical order as shown in Fig. 105, one occurring on each side of the peduncle. In Fig. 102 a distinct area is seen, from the anterior surface of which the cirri spring, and from the borders of which the scaled structure of the calcareous shell commences to form This area has the same outline as the stage represented in Fig. 94. The cirri present coarse cilia as long as the diameter of the cirrus; the cavity within is large, on the outer border of which a few irregular granules are arranged in a single line. See Fig. 101, representing a cirrus from stage 102.

This brings the development of Terebratulina up to its "Early Stages," already described by me in these Memoirs.[3]

By comparing the early conditions of the embryo Terebratulina with that of Thecidium, described by Lacaze-Duthiers, a certain resemblance is observed, so far as the division of

[1] See an interesting paper of Prof. King on the structure of the tubules in the test of Brachiopoda, in the Memoirs of the Royal Irish Academy, Vol. XXIV, p. 439.

[2] See De Morgan on the Structure and Functions of the Hairs of Crustacea, Philosophical Transactions, Vol. CXLVIII, p. 805.

[3] Morse. Early Stages of Terebratulina. Mem. B. S. N. H., Vol. II., p 29.

the body into segments, and their power of contracting upon each other is concerned, though the conditions under which they develop will be found to be entirely unlike. The egg of Terebratulina is discarded freely into the water to undergo its development, and possibly its fertilization outside the parent, while the embryo Thecidium is held attached within the pallial cavity, and separates only after it has undergone changes in advance of those found in the embryo Terebratulina after it has become permanently attached.

The presence of eye spots in the embryo Thecidium is another important difference, for though I examined hundreds of the Terebratulina embryos, yet in no instance were the traces of eye spots detected. On comparing the early stages of Terebratulina with that of Discina, we are at once struck by the marked differences between the two; Terebratulina becoming permanently attached by its peduncular segment long before a trace of the peculiar dorsal and ventral plates makes its appearance, or even before any definite structure shows within, while Discina swims freely in the water sometime after the dorsal and ventral plates, cirri, mouth, œsophagus and stomach, have made their appearance.

The long and protrusible œsophagus and head, bearing a crown of eight cirri, or tentacles, in Discina, as described by Dr. Müller, is unlike anything of the kind observed in Terebratulina. Their barbed and deciduous setæ, however, present similar features to those of the embryo Terebratulina.

The embryology of Lingula (which I hope soon to have the opportunity of studying on the coast of North Carolina) will undoubtedly afford stages similar to those observed in Discina. I have already studied, in the transparent plates of *Lingula pyramidata*, the character of the nucleus, and find it perfectly orbicular with a margin finely notched, and in certain fossil Lingulæ I have observed the same orbicular nucleus. With the other characters, in common between Lingula and Discina, we should expect to find similar features revealed in their embryology.

In considering the various degrees of persistence of embryonic features in the few forms we are thus far acquainted with, we are struck with the great difference in this respect between Discina on the one hand, and Terebratulina on the other. Thus, in Discina, attachment takes place sometime after adult characters make their appearance, the peduncle at first extending directly backward, as in Lingula. In Lingula, as I have heretofore observed, attachment never takes place, at least in *L. pyramidata*, the creature living loose in the sand; and this feature will probably be found characteristic of other Lingulæ when they shall have been carefully observed.

Thus we see in later geological forms, attachment taking place earlier in developmental history than in those of earlier geological times. Similarly in earlier geological times we find forms in which the dorsal and ventral plates are chitinous, and, as I have observed in *Lingula pyramidata*, of such transparency that the circulating fluid could be easily seen coursing through the sinuses of the pallial membranes, and in this latter species containing so little earthy matter that when dry they become twisted out of all shape, and even roll up like a leaf. With these facts it requires no hazardous supposition to conceive the primordial Brachiopods devoid of the dorsal and ventral plates, or furnished only with a semilunar membrane on the head, as in that curious annelid Umbellisyllis, described by Sars, and of a form that presented the annelidan characters less disguised by features that have heretofore prevented a right conception of their affinities.

As to the relations of the Brachiopods with the Polyzoa, some features of similarity are

seen between the embryo Brachiopod and the free embryo of Pedicellina, described by Van Beneden,[1] though the development of parts within a cœnœcium, and the formation of statoblasts are features quite unlike the Brachiopod. A roundabout relation might possibly be insisted upon through the Rotifera, in their winter ova.

After this paper had been made up into pages, Mr. Alex. Agassiz called my attention to the fact that Prof. John McCrady had published in the Proceedings of the Elliott Society of Natural History of Charleston, S. C., a notice of a larval Brachiopod.

After a fruitless search among the libraries of Boston for a perfect set of the Proceedings of this Society, I learned that within a week Mr. McCrady had made his home in Cambridge, having recently become connected with the Museum of Comparative Zoölogy. From him I learned that the original description and drawing was presented before the Elliott Society, at its meeting June 15th, 1860, but, owing to the war, had never been published by the Society. In the destruction of Columbia, S. C., by Sherman's Army, Prof. McCrady not only lost his valuable library, but all of his scientific records, drawings and notes. After this irreparable loss, he drew up from memory a description of this Brachiopodan larva, and now generously allows me to make free use of this valuable manuscript, which contains the first and only observations on a larval Lingula ever made.

The creature in question was found by him either late in the fall of 1859, or in the spring of 1860, he cannot now remember which. It was found off Sullivan's Island in Charleston Harbor. The following is quoted from his manuscript.

"1st. The larva is a free swimming animal.

"2d. Its means of locomotion are large vibratile cilia, clothing the cirri of the arms, precisely as in Bryozoa.

"3d. It was provided with a bivalve semi-transparent horny shell, recalling the shell of Lingula, but with no trace of a foot stalk." (Mr. McCrady adds in pencil that the form of the shell was flattened, and more ventricose than that of adult Lingula.)

"4th. In motion the valves were opened just enough to allow free play to the ciliated cirri of the arms, which (*i. e.*, the cirri) was thrust out beyond the shell rim.

"5th. The arms were never extended beyond the shell rim, but just within and along their margin.

"6th. The opacity of the body was such, that added to the cloudy semi-transparency of the horny shell, it was impossible to make out other details.

"7th. When the larva ceased swimming, the arms and their cirri were retracted, the valves closed, and the animal sank to the bottom."

By comparing the above description with that of Dr. Fritz Müller's description, given in the first part of this memoir, the closest similarity will be observed between them in their general appearance, their mode of swimming, and even to the manner in which, when at rest, they close their shells and sink to the bottom of the vessel in which they are confined. Mr. McCrady assures me he has never seen Müller's description of the larval Discina.

It is interesting to remark that nearly at the same time, these two naturalists should make the first observations ever made on the embryology of the Brachiopods, if we except the very brief notice of Oscar Schmidt.

[1] Hist. Nat. du genre Pedicellina. Mém. Acad. Royal de Belgique. Tome XIX.

The expression of mine which occurs above, that the embryology of Lingula when known would agree with that of Discina, was in type long before I became aware of Mr. McCrady's discovery.

The absence of setæ in the embryo, with the opacity of the valves, is an evidence that it was considerably advanced, for Müller described some of the larva observed by him as having lost the larger bristles.

In closing this brief memoir I wish to express my thanks to Mr. Richard Rathbun, who accompanied me to Eastport, and who assisted me in securing materials for study.

To Mr. Edward Burgess I am again under many obligations during the preparation of the paper.

My thanks are also due to Mr. Chas. A. Walker, who has with great fidelity and patience reproduced accurately my drawings upon steel.

Explanation of Plates.

PLATE VIII.

Fig. 1. A cluster of eggs from the genital band.

Fig. 2. A single egg encased in its capsule.

Figs. 3, 4, 5. Eggs from the perivisceral cavity immediately after their escape from the pallial sinuses.

Fig. 6. Highly magnified portion of the eggshell.

Figs. 7, 8, 9, 10 11. Eggs in various stages of segmentation.

Fig. 12. First ciliated stage.

Figs. 13, 14, 15, 16, 17. Successive stages of transverse division of embryo, showing long tuft of cilia at cephalic extremity.

Figs. 18, 19, 20, 21. From a single embryo, showing various outlines assumed while swimming.

Figs. 22, 23, 24. Different views of another embryo.

Figs. 25, 26, 27. Different embryos showing first appearance of caudal or peduncular segment.

Figs. 28 to 36. Different embryos at the stage when the caudal segment becomes conspicuous.

Figs. 29, 30. Representing the same embryo contracted and expanded.

Figs. 37, 38, 39, 40, 41. Embryos just attaching themselves by their caudal segment.

Figs. 42, 43. Drawn from the same embryo: the first showing the embryo stretched to its utmost, the second the same contracted. (These motions would often follow each other rapidly.)

Figs. 44, 45. Embryos showing first appearance of ventral? area by the bulging of the thoracic ring.

Figs. 46 to 53. Embryos in various stages showing widening of thoracic ring, and its gradual growth toward enclosing the cephalic ring.

Figs. 54 to 61. Successive stages of the embryo showing formation of dorsal and ventral areas by the folding and growth of the thoracic ring. In Fig. 61 the head is still seen projecting from the dorsal and ventral folds of the thoracic ring.

Figs. 62 to 77. Succeeding stages of embryos drawn in various positions. The deciduous setæ appear in these stages.

Fig. 68. Dorsal and ventral plates of embryo, the contents having been removed by Paramæcia.

Note. The cilia constantly clothing the embryo have been purposely omitted except in a few cases, to save trouble in engraving. On the first appearance of the dorsal and ventral folds of the thoracic ring, the cilia disappear from that region. Figs. 18 to 77 were drawn with a $\frac{4}{10}$ objective of Smith and Beck; the embryos measure about the $\frac{1}{150}$ inch in diameter.

PLATE IX.

The figures of embryos upon this plate as follows: 78, 79, 80, 81, 82, 83, 85, 86, 87, 88, 89, 90, 91, 92, 93, and 94 were drawn with a Wales ⅛ inch; a few of them are shown less magnified on Plate VIII.

Fig. 78. Free swimming embryo showing first trace of alimentary tract and peduncular segment.

Fig. 79. Free swimming embryo showing deciduous setæ projecting behind. This feature was only observed in two instances.

Fig. 80. Showing widening of thoracic segment, depression of cephalic segment, and first attachment of caudal segment.

Fig. 81. Appearance of embryo Fig. 85 after having been crushed. The embryo shell, apparently corneous, is split at the peduncular end. The membrane representing the head and cephalic wall is bulged out, with ruptures from which the cellular contents of the body are escaping, and the deciduous setæ are separated from their base of support.

Fig. 82. First stage in which the mouth makes its appearance, and dorsal and ventral plates become distinctly marked.

Fig. 83. Earliest stage in which definite internal structure was found. The peduncular segment characterized by thick walls is seen hanging in the thoracic or pallial cavity.

Fig. 84. Highly magnified drawing of deciduous setæ showing their barbe'd character.

Fig. 85. Showing arrangement of deciduous setæ, and contour of embryonic shell.

Fig. 86. Another stage similar to that shown in Fig. 83.

Fig. 87. Showing first bulging of thoracic ring and clear interspace within. This region is characterized by large granules marking its wall, and in first losing its ciliary lining. The bulging probably indicates the region of the larger or ventral valve.

Fig. 88. A stage slightly advanced from Fig. 85, showing change in outline, the anterior margin strongly ciliated. The deciduous setæ were easily dislodged at this stage, and were often lost in examination.

Fig. 89. A portion of shell of Fig. 88 crushed, showing by its fracture a harder consistency.

Fig. 90. Stage showing for the first time a primary cirrus or tentacle upon each side of its head.

Fig. 91. The same crushed, showing fracture of shell, and parts forced out by pressure.

Fig. 92. Stage similar to Fig. 85.

Fig. 93. A slightly advanced stage from Fig. 92, showing widening of anterior margin.

Fig. 94. A stage slightly advanced from the preceding, with a definite structure showing in the anterior portion of shell.

Fig. 95. Adult characters now assumed, permanent setæ now showing, and pallial cœca present.

Fig. 96. The youngest stage met with in which adult characters were present. The permanent setæ, seven in number, project from the anterior margin. The peculiar scaled structure of the shell is just appearing, and the primary pallial cœca are present. Within, the rounded stomach, and four tentacles are shown.

Fig. 97. Head, tentacles and stomach from an advanced stage. Figured particularly to show contour of parts about the head.

Fig. 98. A stage considerably advanced from Fig. 96, showing subsequent widening of the anterior portion of the dorsal and ventral plates.

Fig. 99. A setigerous follicle with its seta.

Fig. 100. *a. b.* One of the primary pallial cœca, showing appearance of fringing hairs. *a.* Showing the position of hairs before being disturbed by a brush, and *b*, the same after having been brushed with a delicate camel's hair pencil. These are from Fig. 105.

Fig. 101. A tentacle, or cirrus from Fig. 102, showing cavity within, and arrangement of calcareous particles, and relative size of cilia clothing it.

Fig. 102. A considerably advanced stage drawn to show relations of embryonic area, which is shaded. This portion corresponds to stage shown in Fig. 94.

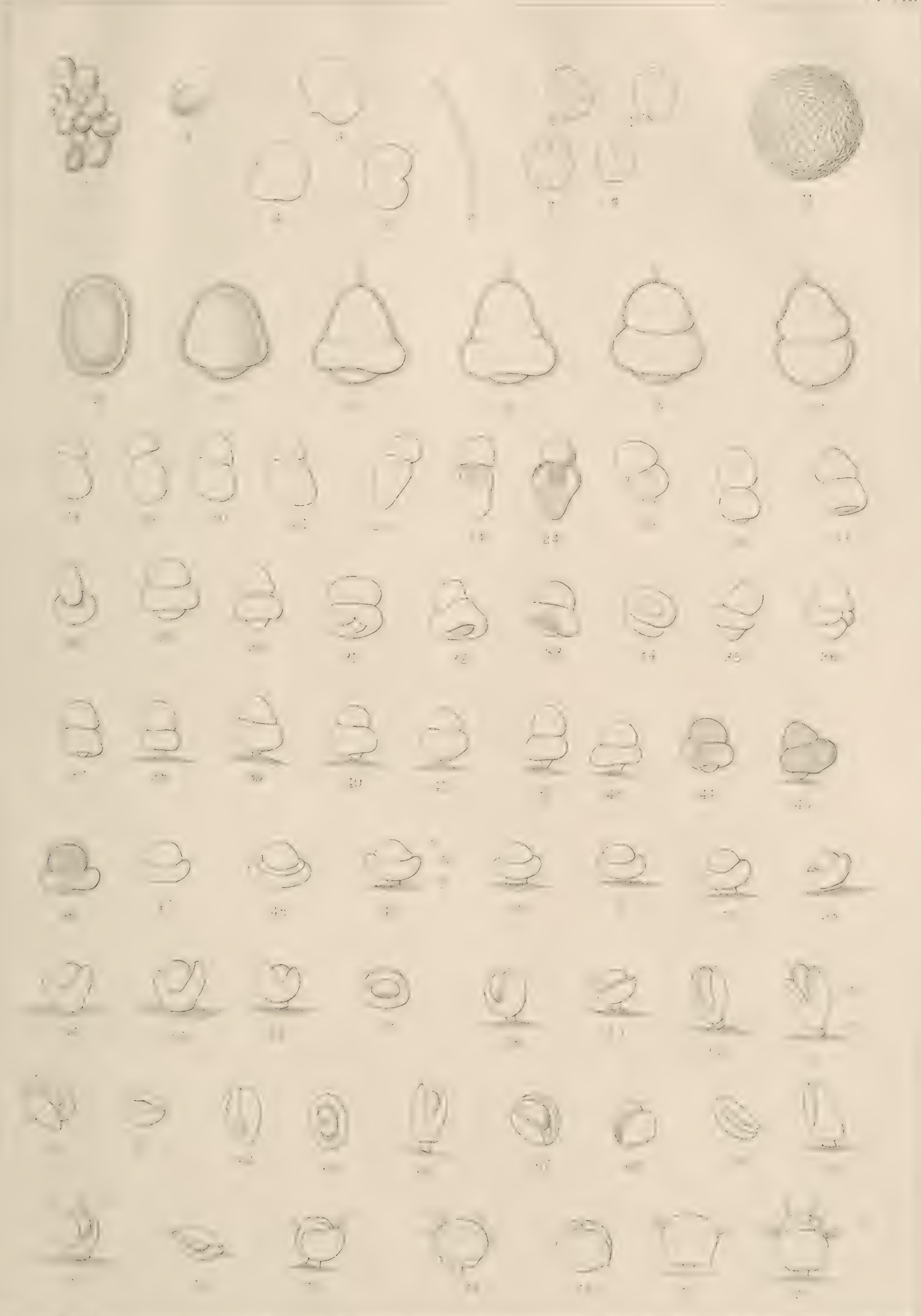
Figs. 103, 104. Showing appearance of fringing hairs bordering pallial cœca.

Fig. 105. Advanced stage to show relative position and size of primary cœca and the first appearance of cœca upon that portion bordering peduncular opening.

In my Memoir on the Early Stages of Terebratulina, published by the Society, I take up the developmental history of Terebratulina from the stage represented in Fig. 105.

EXPLANATION OF LETTERS ACCOMPANYING THE FIGURES.

m, mouth.
œ, œsophagus.
s, stomach.
t, tentacles or cirri.
a, alimentary tract.
pl, pallial cavity.
pv, perivisceral cavity.
pc, peduncular cavity.
c, cephalic segment.
th, thoracic segment.
p, peduncular or caudal segment.
h, head.
ap, anterior parietal wall and head.
e, area of embryonic shell.
f, fold of larger, or ventral area.
pr, primary cœca.
ds, deciduous setæ.
es, embryonic shell.
x, foreign particles adhering to peduncle.



EDW. S. MORSE ON EMBRYOLOGY OF TEREBRATULINA.

G. A. WALKER SC.

EDW. S. MORSE ON EMBRYOLOGY OF TEREBRATULINA.